RESEARCH ARTICLE

Ecology and Reproductive Biology of the Endangered Pondberry, *Lindera melissifolia* (Walt) Blume

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ABSTRACT: *Lindera melissifolia* [Walt] Blume (pondberry) is an endangered woody plant that grows in seasonally flooded wetlands and on the edges of sinks and ponds in six states of the southern United States: Arkansas, Georgia, Mississippi, Missouri, North Carolina, and South Carolina. It is a stoloniferous, clonal shrub up to 2 m in height and is dioecious, with small yellow flowers that bloom in spring. Information on its ecology and reproductive biology is sparse. The species has been affected by habitat destruction and alteration, especially timber cutting, clearing of land, and drainage or flooding of wetlands. Stem dieback was noted in populations in five states, but populations monitored for three years do not appear to be declining. Three fungal pathogens were isolated from stems. Flowers covered with mesh bags produced no fruit, and flowers that received supplemental pollination did not set more fruit than open-pollinated flowers. Seed production was erratic in populations in Mississippi and Arkansas, and no seedlings were noted even after seed production was high. Individual ramets can be easily transplanted and multiply rapidly. Successful dispersal is very limited now due to restrictive land use in areas surrounding pondberry populations and to changes in hydrology. Introduction of plants to new areas may be necessary if the species is to recover.

Ecología y Biología Reproductiva de la Amenazada Pondberry, Lindera melissifolia (Walt) Blume

RESUMEN: *Lindera melissifolia* [Walt] Blume (Pondberry) es una planta leñosa que crece en humedales estacionalmente inundados y en los bordes de cauces y lagunas en seis estados: Arkansas, Georgia, Mississippi, Missouri, Carolina del Norte, y Carolina del Sur, en el Sur de E.E.U.U. Es un arbusto clonal, estolonífero de hasta dos m de altura y es dióico, con pequeñas flores amarillas que aparecen en primavera. El conocimiento de su ecología y su biología reproductiva es escaso. La especie ha sido afectada por la destrucción y alteración de hábitat, especialmente por corta de madera, limpiado de tierras y por el secado o la inundación de humedales. Se notaron troncos muertos en poblaciones de cinco estados, pero las poblaciones monitoreadas durante tres años no parecen estar disminuyendo. Tres hongos patógenos fueron aislados de los troncos. Las flores cubiertas con bolsas de malla no producieron frutas, y las flores que recibieronn polinización suplementaria no producieron más frutas que las polinizadas normalmente. La producción de semillas fue errática en las poblaciones de Mississippi y Arkansas, y no se han observado plántulas aun después de alta producción de semillas. Ramets individuales pueden ser transplantados fácilmente y se multiplican rápido. La exitosa dispersión está limitada ahora por el uso restrictivo de la tierra en las áreas cercanas a las poblaciones de pondberry y por los cambios hidrológicos. La introducción de plantas en nuevas áreas puede ser necesaria si se pretende recuperar la especie.

Index terms: bottomland hardwoods, endangered species, *Lindera melissaefolium, Lindera melissifolia*, pondberry

INTRODUCTION

Lindera melissifolia (Walt) Blume (pondberry), a member of the Lauraceae, is a stoloniferous, clonal shrub up to 2 m tall that occurs in seasonally flooded wetlands, and on the wet edges of sinks, ponds, and depressions in the southeastern United States (Radford et al. 1968). Pondberry has probably always been a rare species (Steyermark 1949, Kral 1983), and knowledge of its ecology and reproductive biology is limited. Morgan (1983) reported that flower and fruit production were highly variable. At present there are populations in Arkansas, Georgia, Mississippi, Missouri, North Carolina, and South Carolina; it is apparently extirpated from Alabama and Louisiana and possibly Florida. The distribution and abundance of pondberry have been affected by habitat destruction and alteration, especially timber cutting, clearing of land, and drainage or flooding of wetlands. The species was listed as endangered by the U.S. Fish and Wildlife Service in 1986 (U.S. Fish and Wildlife Service 1986). Many of the existing pondberry colonies are small, and occupy only a portion of the apparently suitable habitat. Although the pondberry federal recovery plan states that there are 36 extant populations (U.S. Fish and Wildlife Service 1993), new colonies have been discovered since 1993, some in new locations, and some near known populations. Some populations that were thought to be separated by enough distance to preclude interbreeding (as on the Delta National Forest, Miss.) may be linked by recently discovered colonies.

Pondberry usually occurs in clones of numerous stems with erect or ascending shoots and few branches (Figure 1). The species is dioecious, with small yellow flowers that bloom in spring before leafout. The fruit is a red drupe about 1 cm long that matures in late summer or fall. Female clones are smaller than male clones and are sometimes absent from stands (Wright 1989, 1990). As in many clonal species, seedlings are rarely observed (Wright 1990). Stems flower in the second to fourth year of growth but usually die by the sixth or seventh year, and are replaced by new stems that grow from the base of the plant (U.S. Fish and Wildlife Service 1993). A mature colony often consists of a mixture of live and dead stems (U.S. Fish and Wildlife Service 1993). Stem dieback, in which the tops of stems die and the ramets eventually die down to the ground, is not well understood in this species (Godt and Hamrick 1996). Some pondberry populations are more severely affected than others, and it is not clear whether this reflects the natural aging process or whether it is caused by disease or climate (Godt and Hamrick 1996). Robert McCartney (Woodlanders, Inc., Aiken, S.C., pers. com.) reported that the fungus *Phomopsis* was isolated from dieback stems of pondberry in South Carolina in 1985.

The purpose of this study was to describe the ecology and reproductive biology of pondberry as an aid in conserving the species and bringing about its recovery. It will be necessary to eventually establish new populations in order to meet objectives of the recovery plan (U.S. Fish and Wildlife 1993), which states that the species will be downlisted from endangered to threatened status when 15 protected, self-sustaining populations occur throughout the species' historic range. This study was designed to answer several questions that are related to establishment and spread of pondberry populations. One question was: How specific are the habitat requirements of the species? We also wanted to investigate the causes of stem dieback, specifically does dieback occur in only some populations or is it widespread, and should populations with dieback be avoided when seeds or stems are collected for use in introduction to new areas? The other specific objective of the study addressed a series of questions about reproduction: What causes failure of flowering and fruiting? Is seed production pollinator limited? Can individual stems be easily transplanted? How difficult is it to obtain propagules for translocation to new areas?

STUDY SITES AND METHODS

Pondberry sites in five states were visited and the habitat was characterized. Reproductive biology of populations of pondberry was studied at two sites in Arkansas and one site in Mississippi and data was collected on dieback from these populations and from Bolivar County, Mississippi. Several additional populations in Arkansas, Georgia, and South Carolina were censused for dieback.

One Mississippi population is on private land in Bolivar County, in a low wooded area that floods in winter and spring. The small area (79 ha) is surrounded by agricultural land. The pondberry population is very large, with thousands of tall stems. Dominant tree species include water oak (*Quercus nigra* L.), sugarberry (*Celtis laevigata* Willd.), and hickories (*Carya* Nutt. spp.); trees are not large, but provide some shade. Poison ivy (*Toxicodendron radicans* L. Kuntze) is abundant in the understory; greenbriars (*Smilax* L. spp.), ladies' eardrops (*Brunnichia ovata* [Walt.] Shinners), and swamp milkweed (*Asclepias perennis* Walter) are also present.

The other Mississippi population we studied occurs on the Delta National Forest (Delta NF) in Sharkey County on the Red Gum Research Natural Area. The forest is intersected by drainages and sloughs, and seasonal flooding occurs from late fall to spring. The land is nearly flat, but a difference in elevation of 25–50 cm in northwest Mississippi can result in a change of species composition. The Red Gum Research Natural Area is a 16.2-ha remnant of virgin forest; it is slightly higher in elevation than most of the Delta NF and is only occasionally flooded. Soils belong to the Sharkey-Alligator-Dowling associations. The dominant tree species include sweetgum (*Liquidambar styraciflua* L.), box elder (*Acer negundo* L.), sugarberry, and American elm (*Ulmus americana* L.) (Devall and Ramp 1992). Principal species of the shrub layer are palmetto (*Sabal minor* [Jacq.] Pers.) and cane (*Arundinaria gigantea* [Walt] Muhl.). The pondberry population is much smaller and more scattered than the one in Bolivar County, and ramets are smaller. Most stems are growing in shade.

The Arkansas populations occur in the northeastern part of the state. The plants grow as shaded understory shrubs around temporary ponds in bottomland hardwood forests. These sandhill ponds in the northernmost part of Arkansas and southern Missouri are dominated by pin oak (*Quercus palustris* Muenchh.), (Phillip Moore, Arkansas State Highway and Transportation Department, Little Rock, pers. com.). The ponds occur in depressions between old dunes, which were formed from glacial outwash (Saucier 1978). Due to erosion, the surrounding land is now almost level, and most of it is farmed, except for the low areas where the ponds occur. Ponds fill in winter to a depth of 50 cm or less, and usually retain water until after leafout. The pondberry populations are usually well isolated from each other because of the topography and the agricultural fields surrounding most ponds (Wright 1989, 1990; Richardson et al. 1990). Soils are usually loams and silty loams of the Boskett-Tuckerman series (U.S. Fish and Wildlife Service 1993) and are rather acidic. The sole pondberry population in Missouri is at the southern border of the state and is contiguous with the Corning, Ark., population.

Pondberry populations on the Francis Marion NF in South Carolina occur in limestone areas, usually growing near sinkholes surrounded by pondcypress (*Taxodium distichum* var. *nutans* [Ait.] Sweet), with practically no other species in the understory. Some mature pondberry stems at the sinkholes are only a few centimeters

Figure 1. (a) Flooded pondberry in flower showing clusters along stem, (b) almost mature pondberry fruits, (c) extensive pondberry population growing in nearly full sun in Georgia, (d) dead stems resulting from dieback or environmental conditions.

in height. However one thriving population occurs in full sun in an open area with abundant chain fern (*Woodwardia* Smith sp.) and grasses.

Pondberry populations in Georgia occur around the borders of sphagnum bogs. There is an extensive, thriving population around a sphagnum bog in Wheeler County. Tree species present include maple (*Acer rubrum* L.), sweetgum, and loblolly pine (*Pinus taeda* L.). The site is very open and the pondberry stems are nearly in full sun. *Litsea aestivalis* (L.) Fern (pond spice), another rare member of the Lauraceae, is present here and at another nearby pondberry location.

Dieback

Numbers of healthy stems (the extent of clones is unknown), stems with dieback, and dead stems were counted in 1-m x 1-m quadrats 3 m apart along north–south and east–west transects through the populations. The north–south transect was placed randomly, and the east–west transect was placed midway along the first transect and perpendicular to it. Operationally, dieback stems were defined as those with green leaves at the base but with the distal portion dead and brown. At each location, the height of 15 stems in each category was measured.

Differences in mean height between groups were determined by one-way ANOVA, and means were separated by Student-Newman-Kuels (SNK) test. If variances were not equivalent, a Kruskal-Wallis one-way ANOVA on ranks was performed with means separated by SNK test. Differences in the numbers of live, dead, and dieback stems between samples were assessed by heterogeneity chi-square. The ratio of live to dead to dieback stems for each sample was compared to the ratio of live to dead to dieback stems for all the samples added together (4367:1152:2028) to determine if each sample could have been randomly drawn from a single, large, homogeneous population. Heterogeneity for populations that were sampled more than twice was assessed in the same manner to see if ratios of live to dead to dieback stems changed over time. Statistics were calculated using SigmaStat (SigmaStat 1992–1994).

Microorganisms Isolated from Pondberry

Diseased pondberry stems were collected near Corning, Arkansas, in March 1999. Stem sections (0.5 cm) were surface-sterilized for 5 minutes in 10% by volume of laundry bleach containing 0.525% by weight sodium hypochlorite in sterile distilled water. Sections were then rinsed in sterile distilled water, and five sections were placed in plastic petri dishes containing potato dextrose agar (PDA) amended with the antibiotics chloramphenicol (0.75 mg L^{-1}) and streptomycin sulfate (1.23 mg L^{-1}). The plates were placed in a fluorescent-lighted incubator (12 h light/dark) at 25° C for 4 days (Tuite 1969).

Fungal hyphae began emerging from the surface-sterilized stem sections after 1–2 days. After 4 days, distinct fungal colonies had formed. Colonies were examined for fruiting structures (spores or conidia) at 20X with a stereomicroscope. From fungal colonies in which fruiting structures had formed, small sections were excised with a dissecting needle, placed in a small water droplet on a microscope slide, and examined at 100X with a phase-contrast microscope. Isolated fungi were identified to genus.

Reproductive Biology

During flowering, plants at each location (>220 plants/site) were tagged, flowers were observed, and the gender was noted.

Table 1. Number of healthy stems, dead stems, and stems showing signs of dieback for pondberry populations in the southern United States and heterogeneity analysis. Percentage of total stems is in parentheses.

Site and Date	Healthy Stems	Dieback Stems	Dead Stems	Chi Square (*P*) (df =2)
Bolivar Co., Miss.				
6/2/98	313 (47.2)	224 (33.8)	126 (19.0)	151.3 (0.0001)
8/21/98	111 (37.0)	42 (14.0)	147 (49.0)	73.3 (0.0001)
7/22/99	316 (62.6)	54 (10.7)	135 (26.7)	8.4 (0.0149)
9/16/99	357 (44.5)	164 (20.5)	281 (35.0)	52.7 (0.0001)
12/10/99	188 (34.8)	40 (7.4)	313 (57.9)	236.5 (0.0001)
7/6/00	421 (61.6)	65 (9.5)	197 (28.8)	16.4 (0.0003)
Delta NF, Miss.				
6/16/98	82 (69.5)	24 (20.3)	12 (10.2)	16.8 (0.0002)
7/22/99	70 (79.5)	11 (12.5)	7 (8.0)	19.2 (0.0001)
9/20/99	164 (83.7)	18 (9.2)	14 (7.1)	56.4 (0.0001)
12/2/99	54 (48.6)	37 (33.3)	20 (18.0)	27.8 (0.0001)
5/26/00	68 (77.3)	13 (14.8)	7 (7.9)	17.3 (0.0002)
8/8/00	81 (72.3)	20 (17.9)	11 (9.8)	16.5 (0.0003)
Corning SL, Ark.				
8/2/99	629 (73.0)	77 (8.9)	156 (18.1)	73.9 (0.0001)
9/28/99	506 (52.3)	159 (16.4)	303 (31.3)	11.6 (0.003)
8/3/00	579 (75.7)	75 (9.8)	111 (14.5)	92.4 (0.0001)
Corning TR, Ark.				
8/2/99	141 (67.8)	26 (12.5)	41 (19.7)	8.34 (0.0155)
9/28/99	126 (61.8)	31 (15.2)	47 (23.0)	1.61 (0.4467 NS)
12/07/99	81 (46.6)	43 (24.7)	50 (28.7)	13.8 (0.001)
5/22/00	44 (59.5)	12 (16.2)	18 (24.3)	0.25 (0.8813 NS)
8/03/00	36 (42.4)	17 (20.0)	32 (37.6)	8.4 (0.0154)

Table 2. Mean heights (cm) of healthy stems, dead stems, and stems with dieback of pondberry *(Lindera melissifolia)* at four sites in Arkansas and Mississippi. Standard errors in parentheses.

Site and Date	Healthy Stems	Dieback Stems	Dead Stems	MSE*
Bolivar Co., Miss.				
6/9/98	63.6 (6.2)b	168.2 (4.4)a†	127.3 (4.8)c	41683.0
9/16/99	89.9 (15.3)	122.7 (12.7)	127.3 (12.5)	NS
12/10/99	42.0 (5.9)a	82.3 (11.8)b	135.5 (11.8)c	32964.9
7/6/00	112.3 (6.3)a	154.8 (9.6)b	144.3 (8.7)b	7360.1
Delta NF, Miss.				
6/16/98	62.5 (5.0)a	72.2 (2.8)a	100.9 (6.7)b	KW‡
9/20/99	81.7 (7.5)b	86.1 (7.5)b	58.3 (3.1)a	3349.4
12/2/99	92.6 (8.3)b	102.1 (6.1)b	64.4 (6.0)a	5774.8
5/26/00	96.9 (3.5)b	60.6 (6.1)a	83.0 (4.8)b	3174.4
8/8/00	95.3 (3.5)	87.3 (4.8)	86.1 (6.1)	NS
Corning SL, Ark.				
9/28/99	125.5 (13.7)a	91.9 (11.6)a	119.1 (5.9)a	KW
12/7/99	102.4 (7.8)	97.1 (10.3)	87.6 (6.7)	K.W.
5/22/00	106.1 (8.7)	86.7 (6.9)	80.3 (7.9)	NS
8/3/00	109.3 (5.6)	109.5 (8.5)	100.3 (7.7)	NS
Corning TR, Ark.				
9/28/99	94.6 (5.86)a	100.4 (8.52)a	86.9 (9.32)a	691.5
12/7/99	85.7 (7.6)	86.1 (7.3)	70.7 (7.1)	NS
5/22/00	92.7 (9.1)	85.6 (7.0)	72.4 (6.7)	NS
8/3/00	88.8 (4.2)	89.6 (5.1)	102.1 (5.6)	NS

* Mean Square Error; NS = not significantly different at 0.05 level.

† Values in rows followed by a different letter are significantly different at 0.05 level.

‡ Kruskal Wallace one-way ANOVA on ranks.

Flower clusters on male (10–15 clusters/plant) and female (6–12 clusters/plant) plants and the number of flowers/cluster were counted. Flower clusters were covered with mesh bags to exclude pollinators. All flowers on one stem of each of eight plants were hand-pollinated with pollen from nearby staminate flowers, using an artist's brush. A stem with open-pollinated flowers on each plant was chosen as a control. Two months later, fruit were counted on all tagged plants.

Propagules for Translocation

In August 1998, 10 young pondberry stems from a population in Mississippi were dug and planted in pots using soil from the area in which they grew; these were maintained in the greenhouse.

RESULTS

Dieback

Numbers of healthy, dead, and dieback stems, and the percentage of total stems for each sample, are listed in Table 1. In 18 of 20 samples there were more live than dead or dieback stems and in 13 of 20 samples there were more live stems than dead and dieback stems together. The total heterogeneity chi-square for numbers of stems was highly significant (chi-square = 424.8 df = 10, P<0.0001). The ratio of live to dead to dieback stems for 18 of 20 populations was significantly different than the ratio of all the populations pooled together (4367:1152:2028). Over time the percent of dieback stems at the Bolivar County, Mississippi, site decreased significantly (chi-square = 118.7, $P >$ 0.0001) and did not change for the Delta NF and the Corning SL sites. The percent of dieback for the Corning TR site increased from 12.5% to 20% (chi-square = 16.6, P = 0.0003), but this frequency is within the range observed in other populations (e.g., Bolivar County 6/2/98). The heights of dieback stems ranged from 60.6 to 168.2 cm, healthy stems from 42.0 to 125.5 cm, and dead stems from 58.3 to 144.3 cm (Table 2). The tallest dead or dieback stems were in Bolivar County in partial shade, and the tallest live plants were from the Corning SL, Arkansas, site in almost complete shade.

Microorganisms Isolated from Pondberry

Three fungal species were isolated (*Cercospora*, *Diaporthe*, and *Colletotrichum* [= *Gloesporium*]) that were previously reported from *Lindera* (Table 3). Pathogens reported from spicebush (*Lindera benzoin* [L.] Blume) include *Botryosphaeria ribis* var. *petersi*, *Cercospora petersi*, *Diaporthe sociata*, *Dothidea linderus*, *Gloesporium falcatum*, *Hendersonia linderae*, *Hymenochatae applutinans*, *Helminthosporium petersi*, *Microdiplodia linderae*, *Nectria ochroleuca*, *Phyllostica linderae*, *Valsa linderae*, *Solenia anomala*, and *Trametes malicola*; *Asterina ramularis*, *Physalospora obtusa*, and *Phymatrichum omnivorum* were reported from pondberry and spicebush (Anonymous 1960). Nomenclature

Table 3. Fungi isolated from diseased pondberry (*Lindera melissifolia*) collected from Corning, Arkansas, 1999.

Fungus	Colonies per plate (avg.)	Fungus	Colonies per plate (avg.)
Alternaria spp.	12	*Colletotrichum* sp.	7
Aspergillis sp.	14	*Fusarium* spp.	10
Diaporthe sp.	8	*Mucor* spp.	8
Cercospora sp.	3	*Phomopsis* sp.	6

follows Barnet and Hunter (1972) and Clements and Shears (1957). *Alternaria* and *Fusarium* were not listed as pathogens, but were common in our observations. Because pondberry is an endangered species, we were unable to reinoculate or collect seed for propagation in order to fulfill Koch's postulates for positive identification of pathogen(s).

Reproductive Biology

Plants were easy to sex during flowering, fruiting, or when pedicels of the previous year's fruit were present. Radford et al. (1968) stated that *Lindera* is dioecious or polygamodioecious, but we did not observe any polygamodioecious plants. Male stems were more common than female stems in the large pondberry populations. Several small pondberry colonies occur near these populations, and in some of them only a few male stems are present.

At the Delta NF site in 1999 all the blooming stems were tagged: 206 male and 17 female stems (Table 4). Male stems produced 10.9 flower clusters per stem. Female stems produced 6.4 flower clusters per stem, with 4.0 flowers per cluster. On 6 October there were 0.8 mature fruits per female stem (3.2% fruit set). At the Corning SL, AR, site in 1999, 161 female stems and 134 male stems were tagged. Thirty-five male stems produced 15.0 flower clusters per stem and 6.8 flowers per cluster. Female stems (132) produced 12.3 clusters per stem and 5.8 flowers per cluster. On September 28 there were 11.5 mature fruits per stem (16.2% fruit set). Six flower clusters (mean 9 flowers/cluster) covered with mesh bags produced no fruit. A *t*-test demonstrated that the number of fruit produced by flowers with hand pollinations was not significantly different from open-pollinated flowers (P = 0.87, df = 10, t = 0.17). Although numerous fruits were produced in the populations, no seedlings were noted. In spring 2000, no fruit were recorded on stems that had flowered the previous year or on other stems at the Corning, Arkansas, site.

At the Bolivar County, Mississippi, site in 1998, numerous fruits were produced (100 fruits were collected, but individual stems were not monitored). In March 1999, stems with buds died suddenly after an ice storm, and only two stems with flowers were noted in the large population. No fruit was produced. In 2000, plants with flower buds were healthy on 20 January but were dead on 10 February. Temperature equipment at the site recorded a low of 22° C on 26 January after weeks of moderate weather.

Propagules for Translocation

The ten transplanted stems grew well in the greenhouse. Four months after transplanting, new stems were growing in every pot (mean 3.2 new stems per plant, standard error = 0.51). The height of these sprouts ranged from 2.5 to 28 cm (mean 10.9 cm, SE = 0.90). One year after transplantation, the mean number of stems had increased to 7.2 per clone (SE = 0.85) with a mean height of 33.2 cm (SE = 5.8, range = 13 to 138 cm).

DISCUSSION

In Mississippi, pondberry occurs in bottomland hardwood forest, while in northeastern Arkansas and southeastern Missouri it is found on the bottoms and edges of shallow seasonal ponds in old dune

Table 4. Flowering and fruiting of pondberry (*Lindera melissifolia*). In 1999, fruit was counted on 5/20(1) and 9/28(2) in Ark. and on 4/22(1) and 10/6(2) in Miss. In 2000, fruit was counted on 5/22 in Ark. and on 5/26(3) and 9/12(4) in Miss. Standard errors are in brackets.

	Corning SL, Arkansas		Delta NF, Mississippi	
	Male	Female	Male	Female
Stems, Flower Clusters/Stem	35, 15.0 [1.59]	132, 12.3 [0.78]	206, 10.9 [0.97]	17, 6.4 [1.47]
Flowers/Stem, Flowers/Cluster	102.1 [10.84], 6.8	71.0 [4.78], 5.8		25.6 [6.65], 4.0
Fruit/Stem, Fruit/Cluster (1) % Fruit Set in parentheses		24.1 [1.97], 2.0 (34.0)		7.4 [2.64], 1.3 (32.1)
Fruit/Stem, Fruit/Cluster (2) % Fruit Set in parentheses		11.5 [1.24], 0.9 (16.2)		0.8 [0.44], 0.1 (3.2)
Stems, Flower Clusters/Stem	23, 8.2 [1.72]	41, 2.3 [0.46]	186, 8.7 [0.97]	12, 8.7 [2.62]
Flowers/Stem, Flowers/Cluster			40.6 [4.92], 4.7	50.4 [15.34], 5.8
Fruit/Stem, Fruit/Cluster (3) % Fruit Set in parentheses		0, 0 (0.0)		14.0 [5.17], 1.6 (27.8)
Fruit/Stem, Fruit/Cluster (4) % Fruit Set in parentheses				8.6 [1.24], 0.9, (9.8)

fields. In South Carolina it occurs in areas with karst topography, around the edges of sinkholes, and in Georgia it occurs along the borders of sphagnum bogs. Ambient light at the different sites ranges from deep shade to almost full sun. Since it is obvious that pondberry can occupy very different habitats as long as its requirements for water are met, it is not clear why the species was rare in the past, before widespread alteration of habitat occurred.

Dieback

The high heterogeneity chi-square shows that our sample populations differ from each other with respect to the ratios of live to dead to dieback stems and that the samples could not all have been drawn from a single homogeneous population. The high heterogeneity for the Bolivar, Mississippi, samples demonstrates that a population can vary significantly over time, though weather conditions may partially explain the changes that occurred there. For example, a freeze in March of 1999 killed nearly all aboveground stems, resulting in a high percentage (62.6%) of healthy stems on 22 July 1999. There were correspondingly few dieback stems, suggesting that dieback is an aging phenomenon as mentioned by Godt and Hamrick (1996). Further evidence that dieback attacks mature stems is that the average height of stems with dieback at the Bolivar site is 132 cm.

Dieback was recorded in pondberry populations in Missouri (contiguous with our Corning, Arkansas, population) during 1980–1983. In 1983, 56% of flowering stems in randomly placed permanent plots died during the growing season and 4% partially died (Morgan 1983). Twenty years later, percent of dead stems ranged from 14.5% to 31.3%, and percent of dieback stems ranged from 8.9% to 16.4%. Although dieback is still present, it does not appear to have caused a decline in the population, which is still growing vigorously. After 3 years of monitoring, the populations at Bolivar County and Delta NF, Mississippi, do not appear to be declining.

Reproductive Biology

In contrast to 1998 when numerous fruits were produced, there was no fruiting in the Bolivar County, Mississippi, population in 1999 or 2000 due to cold weather. Tucker (1984) reported that frost and freezing temperatures result in reduced fruit set. At Corning, Arkansas, fruiting failed in 2000, possibly because of the heavy fruiting in 1999; stems remained healthy. In 1999 flowers covered with mesh bags produced no fruit, suggesting that pollen is not moved by wind. Apparently fruit production at Corning is not limited by lack of pollination: flowers that received supplemental pollination did not set more fruit than open-pollinated flowers. Niesenbaum (1993) found that supplemental pollination did not improve fruit set of spicebush.

We have not observed pondberry seedlings in the wild, but the small pondberry colonies that occur near several larger populations indicate that successful dispersal occurred in the past. Ridley (1930) noted birds that eat spicebush fruits, which are very similar to those of pondberry (Radford et al. 1968), including cardinal (*Cardinalis cardinalis* L.), robin (*Turdus migratorius* L.), red-eyed vireo (*Vireo olivacea* L.), eastern kingbird (*Tyrannus tyrannnus* L.), and hairy woodpecker (*Picoides villosus* L.). Most of the pondberry populations we visited were in small wooded areas surrounded by agricultural fields, where there is little opportunity for successful dissemination and establishment of colonies. In the past, seeds could have also been disseminated by floodwater, but floodwaters are controlled in these areas today. Without human intervention, it is unlikely that new pondberry colonies will be established to replace those lost because of alteration or destruction of its habitat.

Recovery Limitations

The Lower Mississippi Alluvial Valley, in which two-thirds of the present pondberry populations occur (Mississippi, Arkansas, and Missouri populations), is one of the most endangered ecosystems in the United States (Noss et al. 1995). In addition to the loss of forested wetlands cleared for agriculture, flood control projects that separated the Mississippi River and its tributaries from their floodplains have drastically changed hydrological cycles (Stanturf et al. 2000). Construction of drainage ditches and leveling of fields continue to affect the hydrology of pondberry habitats. Pondberry is truly endangered and its status will decline without human intervention. Much of the habitat suitable for dispersal is fragmented today, thus populations that die out usually will not be replaced.

The pondberry situation differs from that of the "classical" endangered species in that there are populations, some with several large colonies, in six states. Schemske et al. (1994) surveyed 91 endangered plants for which data were available, and found that most species occurred in one or a few populations, practically all had very restricted ranges, and nearly all had narrow habitat requirements. Pondberry occurs in more populations and across a broader geographic range than many endangered plant species, but its habitats are highly fragmented (bottomland hardwoods areas in the Mississippi Delta, sandhill ponds in Arkansas). This situation presumably decreases the probability of overall extinction, but individual populations are just as susceptible as those of other endangered species to environmental and biotic factors. One of the risk factors that has not been studied for pondberry is its occurence in a habitat susceptible to invasion by exotic species. For example, Chinese tallow (*Sapium sebiferum* [L.] Roxb.), a woody invader of wetlands in the southeastern United States (Bruce et al. 1997), produced 22,600 seedlings ha^{-1} in a preserve in east Texas.

Present pondberry populations should be protected and maintained, and searches for new populations should continue, but in order for pondberry to recover, new populations will have to be established, either from seedlings or from clones. The ease with which individual stems removed from clones were propagated in our study suggests that this would be an efficient way to generate plants for transplantation experiments without damage to the original clones. The 10 individual stems that we removed from clones in the field produced 72 stems in one year. In this manner we can produce a pool of plants for reintroduction at presumably no cost to wild populations. Advantages over using seedlings include larger plants that can tolerate flooding and environmental conditions and the ability to manipulate sex ratio and genetic diversity. As dieback was evident in all pondberry populations we examined and has persisted for the last 20 years in the Missouri population (Morgan 1983), it should not be considered a limiting factor in the collection of propagules for translocation.

Pondberry's historic range must be accurately determined to meet objectives of the federal recovery plan (15 protected, self-sustaining populations throughout the species' historic range) (U.S. Fish and Wildlife Service 1993). It has been assumed that pondberry was extirpated from Alabama, Florida, and Louisiana (U.S. Fish and Wildlife Service 1993), but it is possible that pondberry never occurred in present-day Florida. McCartney et al. (1989) stated that specimens at the New York Botanical Garden and the Smithsonian Institution, collected by A.W. Chapman in "Florida" and "West Florida" in the 1800s, document the historical presence of the species in the state. However, in the early 1800s, West Florida was a territory that extended to the Mississippi River; it became part of Louisiana (1812), Mississippi (1817), and Alabama (1819) as well as Florida. Chapman's specimens may therefore be from outside present-day Florida. No specimens of pondberry collected by Chapman are at the Smithsonian Institution (R. Russell, Smithsonian Institution, pers. com.). There are only two specimens, lacking collection dates, at the New York Botanical Garden—one labeled "Florida" and the other labeled "West Florida." Perhaps establishment of pondberry in Florida should be reconsidered, since evidence of the species' existence there is weak.

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